

# FINAL REPORT

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by

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1 Short-term ecological response of a marine managed area

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22

23 ABSTRACT

24 The performance of a marine managed area around Coiba National Park (CNP) in  
25 Panama was assessed using before-after data and four measures of predicted change:  
26 biomass of commercial fish species; biomass of higher carnivorous fish species; density of  
27 shellfish species, and live coral cover. Changes in these measures in CNP were compared  
28 with changes at unprotected sites, and with changes amongst non-commercial and lower  
29 trophic level fishes, as reference groups. Commercial, non-commercial and total fish  
30 biomass increased between 2007 and 2009, with the largest increases recorded in  
31 protected areas. The biomass of carnivores and herbivores also rose during the study  
32 period, with protected areas experiencing the largest gains. Planktivore biomass  
33 decreased in protected areas and rose slightly in unprotected areas. Although considered  
34 an area with moderate-to-low enforcement of fishing regulations, total observed carnivore  
35 biomass of 295 kg/1 000 m<sup>2</sup> in CNP was comparable to highly-enforced oceanic MPAs  
36 within the broader region (Cocos and Malpelo islands). For shellfish species, conch and  
37 oyster densities rose significantly in protected areas. Conversely, sea cucumber density  
38 decreased to near the point of local extinction in protected sites. Live coral cover  
39 decreased non-significantly (ca. 15%) between 2002 and 2009 in both protected and  
40 unprotected areas. Thus, the ecological effects of managed areas around CNP are mixed  
41 but with some strong signs of recovery. Some species, notably commercial fishes, have  
42 benefited substantially from existing fishing regulations, but enforcement is critical to full  
43 recovery and can be greatly improved.

44

45 *Keywords:* Panama, Coiba National Park, MPA, resilience, fish biomass, Eastern Tropical  
46 Pacific, trophic cascade

47

48 **1. Introduction**

49

50 Marine resource management has traditionally been based on identifying optimal  
51 harvesting limits for specific target stocks (Hughes et al., 2005). However, the decline of  
52 fish and shellfish populations across the world suggests that these traditional management

53 systems are in many cases misguided. Consequently, ecosystem-directed management  
54 tools that aim to protect large marine areas and ecosystem function are urgently needed  
55 and currently represent a research focus (Crain et al., 2009). Fully and permanently  
56 protected and managed marine reserves represent one of these tools.

57

58 The benefits of marine reserves in terms of protecting organisms and their habitats are  
59 now well characterized. Empirical studies have shown increased abundance, biomass  
60 and density in fish and shellfish species within reserve boundaries (Claudet et al., 2008).  
61 For example, Roberts et al. (2001) reported a threefold increase in the combined biomass  
62 of five commercially important fish species after three years of protection in St Lucia's  
63 Soufrière Marine Management Area. By allowing otherwise exploited species to recover,  
64 marine reserves also preserve genetic variability and restore natural age structures in fish  
65 and shellfish populations. In addition, ecosystem function and integrity are maintained by  
66 conserving biodiversity and key habitats (Roberts et al., 2005).

67

68 Recovery (even if partial) of otherwise exploited species is also predicted to support  
69 fisheries adjacent to a marine reserve. Fishery enhancement occurs through two  
70 mechanisms: "spillover", or the density-dependent emigration of adults and juveniles  
71 across the reserve's borders; and "restocking", increased production and dispersal of eggs  
72 and larvae from within the reserve to external regions (Forcada et al., 2006). Restocking  
73 benefits largely result from prohibiting fishing and other harmful activities that prevent fish  
74 and shellfish from reaching maturity. Allowing marine organisms to live longer and grow  
75 larger (Hawkins et al., 2006) greatly increases their fecundity because of the exponential  
76 relationship between body size and fecundity (Bohnsack, 1990). Several studies have  
77 demonstrated spillover empirically. Tupper and Rudd (2002) established that catch per  
78 unit effort for hogfish decreased with increasing distance from a reserve in the Turks and  
79 Caicos Islands, strongly suggestive of spillover. Similarly, Roberts et al. (2001) found that  
80 spillover of black drum, red drum and spotted sea trout benefited recreational fisheries  
81 adjacent to a wildlife reserve in Florida.

82

83 Supporting ecological function and integrity are recognized as particularly important  
84 aspects of marine reserves because they increase resilience. Resilience is, in theory,  
85 characteristic of marine reserves for various reasons. Firstly, by preventing food-web

86 simplification and the loss of key functional groups like herbivores and top predators,  
87 marine reserves are more stable and less prone to phase shifts (Hughes et al., 2005). On  
88 coral reefs, for example, herbivores such as parrotfish inhibit the growth of macroalgae  
89 that can replace corals; however, top-down limitation may not always have beneficial  
90 outcomes in marine reserves (Mumby et al., 2006). A rise in the abundance of top  
91 predators can trigger trophic cascades, and thus cause a decline in primary and secondary  
92 consumers like parrotfish. If no other herbivores replace those lost to predation,  
93 macroalgae may flourish.

94

95 Although strong evidence is accumulating for the conservation and fisheries benefits of  
96 marine reserves, many people, particularly commercial fishermen and managers, remain  
97 skeptical about their value (Roberts et al., 2005). Indeed, failure to improve adjacent  
98 fisheries through spillover, for example, increases the likelihood that local fishermen will  
99 poach within a reserve (Tupper and Rudd, 2002). Therefore, given the potentially  
100 competing ecological outcomes in marine reserves, any reserve needs to be scientifically  
101 monitored to assess its performance. More information is needed on the basic ecology, life  
102 history and population dynamics of marine organisms to improve the accuracy and  
103 reliability of predictive assessments (Hughes et al., 2005). Time series data are particularly  
104 needed given the paucity of reserve studies that include a temporal component (Willis et  
105 al., 2003), and strong biases in location of reserves that often confound inside-outside  
106 ecological comparisons (Edgar et al., 2004).

107

108 This study aims to evaluate short-term community changes within the initial years of  
109 implemented fisheries regulations in areas under different management regimes by  
110 evaluating changes in various ecological parameters (living coral cover, fish abundance  
111 and biomass, and population density of target exploited species such as lobster conch,  
112 oysters, sea cucumbers). On the basis of theory associated with marine reserves  
113 (Lubchenco et al., 2003), we here test specific predictions that: 1. biomass of exploited  
114 and large carnivorous fish species increase in MPAs relative to external reference sites; 2.  
115 biomass of non-exploited and low trophic level species do not change in MPAs relative to  
116 unprotected sites; 3. densities of targeted invertebrates increase in MPAs relative to  
117 unprotected sites; and 4. live coral cover increases in MPAs relative to unprotected sites.

118

## 119 2. Methods

### 120 2.1. Study area and legal framework

121 The study incorporated nine sites within the marine managed area of Coiba National Park  
122 (CNP) and nine unprotected sites located in the surrounding region of the Gulf of Chiriquí,  
123 western Pacific Panama (Fig. 1). The 18 sites were initially investigated in 2003 and 2007  
124 (Guzman et al., 2004, 2008), and resurveyed in November 2009. CNP was established in  
125 December 1991, its legal status improved in July 2004, and World Heritage recognition  
126 confirmed in July 2005. CNP encompasses an area of 2562 km<sup>2</sup>, with ca. 2025 km<sup>2</sup> (79%)  
127 corresponding to marine environments (Guzman et al., 2004; ANAM, 2009). An interim set  
128 of fishing regulations was implemented while developing the management plan, the most  
129 relevant of which included: (i) the establishment of a **1.8 km no-take zone** around all  
130 islands and islets (ca. 339 km, representing 23.5% of shallow marine environments), (ii) a  
131 ban on all fishing of sharks, lobsters, conch and turtles, (iii) a prohibition on use of fishing  
132 nets, and (iv) maximum numbers and minimum sizes for circular hooks on fishing lines.  
133 Implementation of the management plan was approved in June 2009 (ANAM, 2009). The  
134 geology, climate and oceanography of the area is summarized by Guzman et al. (2004)  
135 and Guzman and Breedy (2008).

### 136 2.2. Fish abundance and biomass

137 Visual censuses of fishes were undertaken using a belt transect protocol implemented  
138 previously for other locations in the tropical eastern Pacific region (see Edgar et al., 2004)  
139 and in April 2007 for Panama. At approximate depths of 5 and 10 m, duplicate 50 x 5 m  
140 transects, separately by 5-10 m, were conducted parallel to the shore at each site. Divers  
141 swam slowly, recording number of species and size categories of all fishes sighted within  
142 each 250 m<sup>2</sup> transect area. Size was estimated within 16 25-mm size-classes (see Edgar  
143 et al., 2009). Fish biomass was estimated from visual abundance counts and size  
144 estimates using length-weight relationships provided for total length of each fish species in  
145 Fishbase (<http://www.fishbase.org>). Fishbase additionally provided dietary information that  
146 was used to categorize fish species into four trophic categories: planktivore, herbivore,  
147 lower carnivore, higher carnivore. Lower carnivores comprised demersal rays and bony  
148 fishes feeding predominantly on crustaceans, molluscs, polychaetes and small (<50 mm  
149 length) fishes. Higher carnivores comprised the sharks, carangids, scombrids,

150 sphyraenids, and larger predatory lutjanids and serranids, feeding on fishes greater than  
151 50 mm length (DeMartini et al., 2008).

152

### 153 2.3. Density of exploited indicator species

154

155 Censuses of lobster (*Panulirus gracilis*), conch (*Strombus galeatus*, *S. peruvianus*), pearl  
156 oyster (*Pinctata mazatlanica*) and common sea cucumber (*Holothuria atra*, *Stichopus*  
157 *fuscus*) were made in February 2007 following survey protocols described elsewhere  
158 (Cipriani et al., 2008; Guzman et al., 2008). Abundance of individuals for each group was  
159 estimated from three replicate belt-transects of 6 x 100 m haphazardly surveyed at two  
160 depths ranging from 1.5-14 m within each site (totaling 6 survey areas of 3 600 m<sup>2</sup> per  
161 site). Transects were visually surveyed, with all individuals counted inside crevices, under  
162 rocks and on sand by two divers using a 6-m long PVC pole as reference, each diver  
163 surveying a half of each transect (a 3-m width strip). Densities per transect were  
164 estimated by dividing the abundance per transect by 600m<sup>2</sup> and scaling to hectares (ha).  
165 The overall mean density of each sampling site was obtained by averaging the density of  
166 all six transects.

167

### 168 2.4. Survey of reef sessile organisms

169

170 Live coral cover and species composition were quantified following a standard belt-  
171 transect protocol (Guzman et al., 2004). Three 10-m long replicate transects were placed  
172 parallel to the coast at two different depths, 1-3 m and 8-10 m at all 19 sites. Coverage of  
173 corals, algae (frondose and turf species) and sponges was visually estimated with a 1m<sup>2</sup>  
174 quadrat divided into 100 cells of 100 cm<sup>2</sup> each. The same total area per site was always  
175 surveyed (90 m<sup>2</sup> per reef or coral community).

176

### 177 2.5. Statistical analyses

178

179 Before-after (2007-2009) comparisons were made using a BACI model Two-way  
180 Repeated Measure ANOVA (sensu Green, 1979) using ln(x+10) transformed data for fish  
181 biomass, square- root for density of indicator species, and arsine for cover of sessile  
182 organisms.

183

### 184 3. Results

185

186 Total fish biomass differed among levels of protection (protected versus unprotected  
187 areas) and years but the interaction was not significant (Table 1). Mean total fish biomass  
188 in the MPA showed a significant 2.5-fold increase between 2007 and 2009, from  $171 \pm$   
189  $46.3$  to  $432 \pm 130.6$  kg/1 000 m<sup>2</sup> compared to unprotected sites (Fig. 2). Biomass of non-  
190 commercial species was only marginally significant among years and between levels of  
191 protection (see Table 1), while biomass for commercial species increased significantly  
192 four-fold in protected sites among years and the year x protection interaction (Table 1).

193

194 In general, higher trophic levels showed between 2007 and 2009 an increase in biomass  
195 inside the MPA while remaining relatively unchanged in unprotected sites (Fig. 3). A  
196 significant five-fold increase, from  $43.44 \pm 20.6$  to  $223.4 \pm 110.9$  kg/1 000 m<sup>2</sup>, was  
197 observed for higher carnivores mean biomass and a three-fold for herbivores, from  $25.1 \pm$   
198  $6.6$  to  $78.3 \pm 11.6$  kg/1 000 m<sup>2</sup>. The protection level x year interactions were significant and  
199 marginally significant for herbivores and higher carnivores, respectively (Table 1). Mean  
200 biomass for lower carnivores and planktivores showed no significant change between  
201 2007 and 2009, nor the interactions (Table 1). All trophic levels were significantly higher  
202 when comparing biomass between protected and unprotected areas in 2009 (Fig. 3). A  
203 detailed analysis of higher carnivores mean biomass inside the MPA indicated that  
204 increases occurred amongst all heavily targeted fish families, albeit with a significant  
205 change only found for lutjanids (six species), from  $5.3 \pm 3.3$  to  $42.6 \pm 18.9$  kg/1 000 m<sup>2</sup> ( $t =$   
206  $3.155$ ,  $p=0.014$ ) because of high variability between sites. Large but non-significant  
207 changes were found for carangids (eight species):  $9.3 \pm 6.9$  to  $80.8 \pm 53.2$  kg/1 000 cm<sup>2</sup>;  
208 sharks:  $20.0 \pm 20.0$  to  $69.3 \pm 52.4$  kg/1 000 cm<sup>2</sup>; and serranids (three species):  $2.2 \pm 0.6$  to  
209  $4.61 \pm 1.0$  kg/1 000 cm<sup>2</sup>.

210

211 Mean population density for all shellfish species but sea cucumbers showed a statistically  
212 non-significant increase inside the MPA from 2006 to 2009 (Fig. 4). Mean conch density  
213 showed the most noticeable increase from  $7.7 \pm 4.5$  to  $63.5 \pm 43.0$  ind./ha, followed by  
214  $68.5 \pm 12.6$  to  $100.6 \pm 31.2$  ind./ha for oysters, and  $4.3 \pm 1.9$  to  $8.3 \pm 4.2$  ind./ha for  
215 lobsters. A small increase,  $1.2 \pm 0.9$  to  $9.9 \pm 5.1$  ind./ha, was observed for conchs in

216 unprotected areas. However, mean conch density was only marginally significant among  
217 years (MS = 50.272; F = 4.344;  $p = 0.054$ ) and not between levels of protection (MS =  
218 32.709; F = 2.464;  $p = 0.136$ ) and the interaction (MS = 8.024; F = 0.693;  $p = 0.417$ ). The  
219 increased oyster density was not significant between levels of protection (MS = 3.344; F =  
220 0.139;  $p = 0.714$ ), among years (MS = 1.967; F = 0.275;  $p = 0.607$ ) and the year x  
221 protection interaction (MS = 19.699; F = 2.754;  $p = 0.116$ ). Similarly, lobster density was  
222 not significant between levels of protection (MS = 7.170; F = 2.206;  $p = 0.157$ ), among  
223 years (MS = 0.108; F = 0.153;  $p = 0.701$ ) and the year x protection interaction (MS =  
224 0.385; F = 0.545;  $p = 0.471$ ).

225

226 Mean live coral cover between 2002 and 2009 showed a decrease from  $43.2 \pm 5.7\%$  to  
227  $35.7 \pm 6.1\%$  in the MPA and from  $42.8 \pm 8.6\%$  to  $26.4 \pm 4.9\%$  in unprotected areas (Fig. 5),  
228 mainly *Pocillopora damicornis* in both areas. However, the differences were only  
229 significant among years (MS = 1245.619, F = 9.546,  $p = 0.007$ ) but not among level of  
230 protection (MS = 226.984; F = 0.357;  $p = 0.559$ ) or interaction (MS = 161.341; F = 1.236;  $p$   
231 = 0.283). Crustose coralline algae cover decreased from  $15.3 \pm 5.0\%$  to  $6.7 \pm 3.1\%$  in the  
232 MPA while remained unchanged in unprotected areas. Nevertheless, differences were not  
233 significant among level of protection, year, and interaction (F = 0.0269,  $p = 0.872$ ; F =  
234 1.711,  $p = 0.209$ ; F = 4.003,  $p = 0.063$ , respectively). Macroalgae cover increased among  
235 years by 16% and 15% in protected and unprotected areas, respectively. Differences  
236 among years were significant (F = 7.528,  $p = 0.014$ ) but no significant change related to  
237 level of protection or interaction was observed (F = 0.633,  $p = 0.438$ ; F = 0.0063,  $p =$   
238 0.938, respectively).

239

#### 240 **4. Discussion**

241

242 The short-term population response was relatively clear across the different studied  
243 organisms and trophic levels, even though statistical significance was generally swamped  
244 by the intrinsic and expected high variability observed between and within sites in an  
245 archipelago with 339 km of the MPA's coastline. Protection from fishing of commercial  
246 species, even over the short time period of this study, had a significant positive effect on  
247 fish biomass, as reported elsewhere (Lester et al., 2009; Molloy et al., 2009). Conversely,

248 protection would appear to influence sea cucumber and lobster abundance much more  
249 slowly.

250 Protected areas had a much larger positive influence on fish biomass by acting as “harvest  
251 refuge” (sensu Acosta and Robertson, 2003) than unprotected areas. Indeed, fish in  
252 protected areas are less vulnerable to fishing and other activities, leading to increased  
253 survivorship and spawning success. The harvest refuge explanation is supported by two  
254 observed patterns for the CNP. Firstly, the largest increases in biomass were observed in  
255 commercial rather than non-commercial fish species. This implies that even short-term  
256 protection without strong enforcement led to reduced fishing mortality in commercial  
257 species, as expected in a harvest refuge. The effect was not as pronounced in non-  
258 commercial species because those species suffer substantially lower fishing mortality, and  
259 so their biomass had not been depressed by fishing as much in the first place. Secondly,  
260 the slight increase in fish biomass in unprotected areas possibly suggests spillover from  
261 protected sites. Spillover and increased recruitment are also predicted in areas that act as  
262 refuges for spawning stocks.

263 A consequence of the observed recovery of fish species was the establishment or  
264 strengthening of predator-prey interactions. In the CNP, the higher biomass of commercial  
265 (predatory) fish species may lead to increased predation of herbivorous and planktivorous  
266 (non-commercial) species. Interactions of this kind may cause trophic cascades -  
267 predator-prey effects that change a species' abundance or biomass across more than one  
268 trophic level (Bascompte et al., 2005). Trophic cascades influence the stability and  
269 structure of entire food webs. It is impossible to determine from the short-term dataset  
270 whether trophic cascades are occurring in CNP. However, it is worth noting that higher  
271 predation may be another cause of the differences in biomass increase between  
272 commercial and non-commercial fish species. Essentially, biomass increases in non-  
273 commercial species could potentially be limited by greater predation pressure from a larger  
274 number of predatory fish. In this context it is worth noting that fish biomass at all but the  
275 lowest trophic levels increased in protected sites while planktivorous fish biomass  
276 declined. Trophic cascades could explain these differences.

277 If cascades are shaping food webs in CNP, it is puzzling that only planktivorous species  
278 were found to be negatively affected. In theory, cascades should also influence

279 herbivores. Stronger interactions possibly occur between carnivores and planktivores than  
280 between carnivores and herbivores, which typically have larger body mass than  
281 planktivores and may thus largely escape predation from recovering populations of  
282 groupers, jacks and snappers. Differences in the strength of cascades may have important  
283 implications for the management of CNP's waters. Interestingly, total carnivore biomass  
284 (higher, demersal, benthic) of 295 kg/1 000 m<sup>2</sup> in CNP, considered here an area with  
285 moderate-to-low enforcement, was comparable to highly enforced oceanic MPAs (Cocos  
286 and Malpelo islands; mean 396 kg/1 000 m<sup>2</sup>) within the Eastern Tropical Pacific region.  
287 Fish biomass was considerably higher than in other weak-enforcement MPA in the region  
288 (mean 116 kg/1 000 m<sup>2</sup>; Edgar et al., in rev.).

289 No clear pattern of change in density was evident across the different shellfish species.  
290 Some species like conch and oyster increased considerably in protected areas, though  
291 patchily between sites. However, sea cucumbers declined to the point where they were  
292 could be considered locally extinct. The lack of a general pattern suggests that the change  
293 in density varied according to the characteristics of each species and the size of existing  
294 populations. Conch density may have increased rapidly in some sites because conch has  
295 life history characteristics that lend themselves to fast population growth. Cipriani et al.  
296 (2008), for example, found that conch populations undergo twice-yearly recruitment events  
297 around the Coiba and Las Perlas archipelagos, a capacity for population growth that is  
298 sufficiently high enough to account for the significant rise in density. It is also possible that  
299 both conch and oyster populations were near a critical threshold size before protection,  
300 above which threshold the population would have grown quickly. Protection may have  
301 allowed the existing populations to rise above this threshold. Indeed, the observed  
302 distribution was partially responding to level of enforcement; high conch densities were  
303 observed in highly patrolled sites even under recruitment limited. We recorded a mean  
304 size (length) of 16.7 ± 0.51 cm (range 4-25 cm) for *Strombus galeatus*, representing adults  
305 and sub adults in the population. Maturity for this species is estimated at age 2.4 year  
306 (Cipriani et al., 2008), thus potential for recovery is high if enforcement is efficient, perhaps  
307 even immediately adjacent to the MPA. We predict a similar outcome for *S. peruvianus*  
308 with a mean length of 11.1 ± 0.33 cm (range 8.5-12.5 cm), but unfortunately, no  
309 information is available on the biology of the species.

310 The two to three year protection period investigated here was insufficient for a detectable  
311 effect on sea cucumber density, possibly due to problems associated with small population  
312 size, life history or ecological traits (Claudet et al., 2010). Nevertheless, with time,  
313 protection should allow sea cucumber populations to recover. Critical thresholds, perhaps  
314 associated with the Allee effect, may also explain the decline in sea cucumber density in  
315 both protected and unprotected areas. The demographic and genetic problems associated  
316 with small population size are well characterized (Caughley, 1994). Cucumber populations  
317 may, then, be suffering from small population effects that are preventing or slowing growth.  
318 A recovery can only occur when population size increases enough to nullify these effects,  
319 our data indicating that more time is needed before this occurs. Finally, Guzman et al.  
320 (2008) found that average densities of Pacific green spiny lobster (*Panulirus gracilis*) in  
321 numerous sites around the Coiba archipelago were extremely low. Indeed, average  
322 densities were comparable to those recorded for over-exploited Caribbean spiny lobster.  
323 Green lobsters are important carnivores that may also require a longer period for recovery.

324 Ecosystems around CNP were most likely in poor condition at the time protection was  
325 established. In particular, reef corals have experienced serious changes and stress over  
326 recent decades (Guzman et al., 2004; Guzman and Breedy, 2008). Yet despite ongoing  
327 damage and stress that has presumably affected ecosystem function, species interactions,  
328 and ecosystem resilience, overall live coral cover remains relatively high at present; mean  
329 of 64% and 28% for coral communities and coral reefs, respectively, an estimate based on  
330 a survey of 24 sites rather than the nine protected sites analyzed here (Guzman et al.,  
331 2004). Regardless, disruption of ecological feedbacks or the loss/reduction of keystone  
332 species in previous disturbance events (e.g., El Niño) appears to have turned CNP  
333 ecosystems into “patchwork ecosystems”, where biological processes and species  
334 interactions are not as strong as in more natural environments. Recovery from a  
335 “patchwork state” will initially occur in small, possibly unrelated steps as suggested by the  
336 high variance between coral reef sites. As an increasing number of interactions and  
337 processes are restored, including trophic cascades, we predict dissimilar recovery patterns  
338 to gradually become uniform (sensu Claudet et al., 2010). For example, the reef shark  
339 (*Trionodon obesus*) showed a 3.5-fold increase in biomass, contrary to other high-enforce  
340 protected areas (Great Barrier Reef) where no recovery or protection in no-take zones is  
341 reported (Robbins et al., 2006).

342 Finally, increasing evidence indicates that marine reserve networks provide resilience  
343 against environmental uncertainty (*sensu* Lubchenko et al., 2003). If a network covers a  
344 sufficiently large area, catastrophes that affect one part of the network are unlikely to  
345 influence other areas. Similarly, the greater the number of habitats protected by a  
346 network, the less likely it becomes that all the habitats in a network are affected by a  
347 catastrophe (Game et al., 2009). The archipelago of Coiba encompasses a convoluted  
348 coastline with numerous islands under protection, representing typical and unusual  
349 habitats that function as a network. The data presented here indicated that the marine  
350 protected area of Coiba National Park (CNP) is showing slow signs of recovery for various  
351 fish and shellfish species from extensive fishing if compared to other unprotected areas of  
352 the Gulf of Chiriquí. However, recovery may not take place entirely because the CNP's  
353 management plan allows fishing in 75% of the MPA, just outside the no-take nautical mile  
354 and including artisanal and sport fishing. Indeed, this continuous artisanal fishing pressure  
355 produced a gross income of US\$ 7.4 million to local fishermen in 2007 (Montenegro 2008).  
356 We conclude that recovery is underway for populations of the most highly exploited  
357 species; however, this recovery is likely hindered by highly depressed state of some  
358 stocks, and the current fishing allowances and low-to-moderate level of enforcement.

359

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450 Table 1. Difference in the mean square values among different level of protection  
 451 (protected and unprotected) and among years (2007 and 2009) and the interactions for  
 452 fish biomass data. Degrees of freedom 1.

		Protection	Year	Protection x Year	
453 454	Total	MS	8.946	2.759	0.59
		F	7.081	12.03	2.576
		P	0.017*	0.003*	0.128
455 456	Non-Commercial	MS	4.274	0.559	0.063
		F	4.39	4.308	0.49
		P	0.052	0.054	0.494
	Commercial	MS	7.65	6.352	2.151
		F	5.72	17.43	5.9
		P	0.029*	0.001*	0.027*
	Higher Carnivores	MS	7.360	4.346	1.395
		F	4.646	13.45	4.317
		P	0.047*	0.002*	0.054
	Lower Carnivores	MS	3.629	0.909	0.057
		F	5.807	3.915	0.326
		P	0.028*	0.065	0.576
	Herbivores	MS	2.518	2.253	1.568
		F	3.285	8.618	5.998
		P	0.089	0.010*	0.026*
	Planktivores	MS	3.031	0.134	0.014
		F	4.207	0.379	0.039
		P	0.057	0.547	0.845
	Lutjanids	MS	1.749	1.028	1.225
		F	4.292	8.790	10.473
		P	0.055	0.009*	0.005*
	Carangids	MS	0.745	0.877	0.300
		F	0.972	4.351	1.489
		P	0.339	0.053	0.240
	Serranids	MS	0.134	0.330	0.008
		F	1.556	8.584	0.219
		P	0.230	0.010*	0.646
	Sharks	MS	0.854	0.341	0.053
		F	2.523	0.726	0.113
		P	0.132	0.407	0.742

457 **List of Figures**

458 Fig. 1. Map of western Pacific Panama showing the distribution of study sites and the  
459 location of Coiba National Park; nine protected 1-9 (all within the 1.8 km no-take zone; not  
460 indicated) and nine unprotected 10-18.

461

462 Fig. 2. Mean ( $\pm$  standard error) before-after fish biomass estimates for total, non-  
463 commercial and commercial species under protected and unprotected management, and  
464 based on total biomass per site.

465

466 Fig. 3. Mean ( $\pm$  standard error) before-after biomass estimates for four trophic levels,  
467 higher carnivores, lower carnivores, herbivores and planktivores under protected and  
468 unprotected management, and based on total biomass per site.

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470 Fig. 4. Mean ( $\pm$  standard error) before-after density estimates for four indicator  
471 (commercial) species under protected and unprotected management.

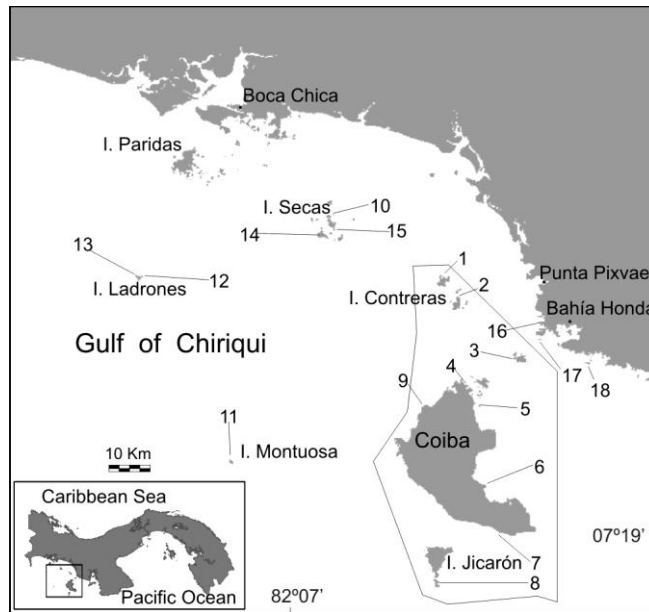
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473 Fig. 5. Mean ( $\pm$  standard error) before-after changes in live coral cover under protected  
474 and unprotected management.

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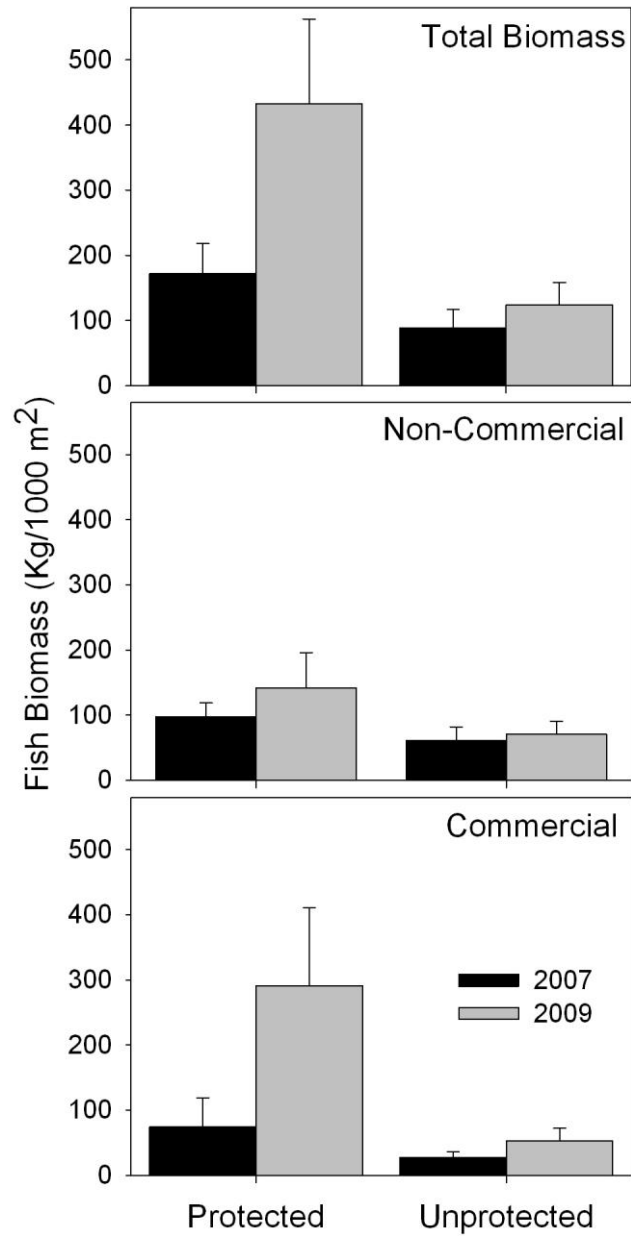
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Figure 1

Map of western Pacific Panama showing the distribution of study sites and the location of Coiba National Park; nine protected 1-9 (all within the 1.8 km no-take zone; not indicated) and nine unprotected 10-18.

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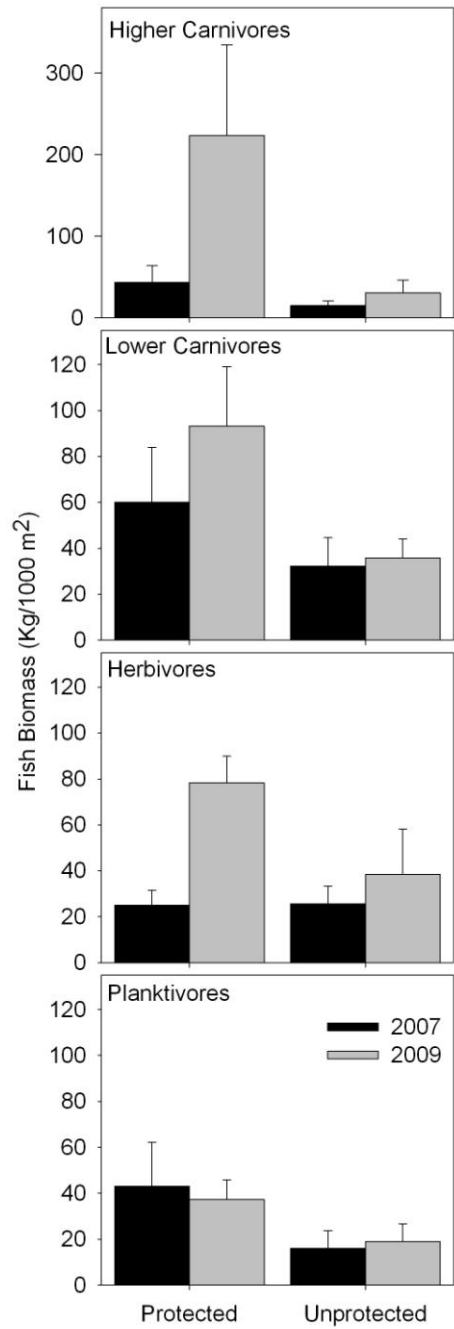


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Figure 2

492 Mean ( $\pm$  standard error) before-after fish biomass estimates for total, non-commercial and  
493 commercial species under protected and unprotected management, and based on total  
494 biomass per site.



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Figure 3

498 Mean ( $\pm$  standard error) before-after estimates for total fish biomass in four trophic levels:

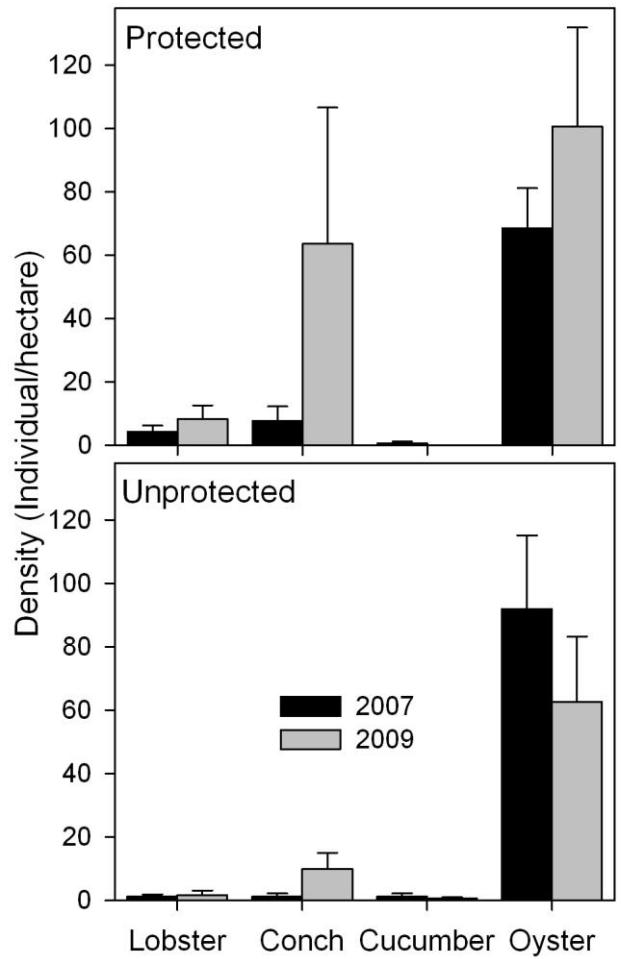
499 higher carnivores, lower carnivores, herbivores and planktivores under protected and

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unprotected management.

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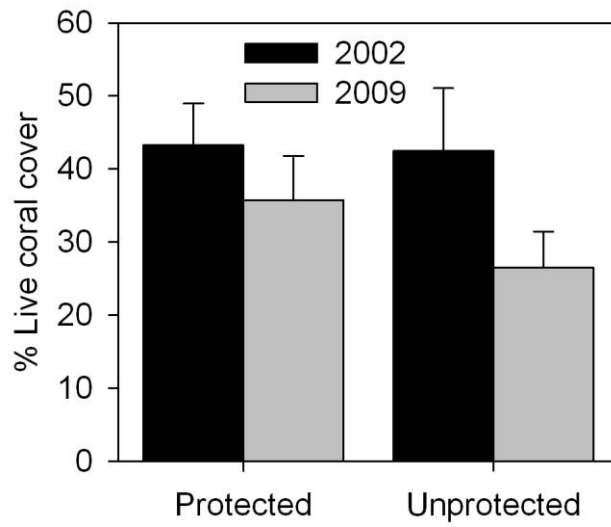
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Figure 4

Mean ( $\pm$  standard error) before-after density estimates for four indicator (commercial) species under protected and unprotected management.

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Figure 5

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Mean ( $\pm$  standard error) before-after changes in live coral cover under protected and unprotected management.

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